Loss of oestrus, concealed ovulation and paternity confusion in free-ranging Hanuman langurs

Michael Heistermann[1]*, **Thomas Ziegler**[1], **Carel P. van Schaik**[2], **Kristin Launhardt**[3]¶,
Paul Winkler[3]† **and J. Keith Hodges**[1]

[1]*Department of Reproductive Biology, German Primate Centre, Kellnerweg 4, 37077 Göttingen, Germany*
[2]*Department of Anthropology and Anatomy, Duke University, Box 90383, Durham, NC 27708-0383, USA*
[3]*Institute of Zoology and Anthropology, University of Göttingen, Bürgerstrasse 50, 37073 Göttingen, Germany*

Ovarian cycles in catarrhine primates are uniquely characterized by prolonged periods of sexual activity in which the timings of ovulation and copulation do not necessarily correspond. According to current hypotheses of primate social evolution, extended sexuality in multi-male groups might represent part of a female strategy to confuse paternity in order to reduce the risk of infanticide by males. We test this hypothesis by examining mating behaviour in relation to timing of ovulation and paternity outcome in a multi-male group of free-living Hanuman langurs. Using faecal progestogen measurements, we first document that female langurs have extended receptive periods in which the timing of ovulation is highly variable. Next, we demonstrate the capacity for paternity confusion by showing that ovulation is concealed from males and that copulations progressively decline throughout the receptive phase. Finally, we demonstrate multiple paternity, and show that despite a high degree of monopolization of receptive females by the dominant male, non-dominant males father a substantial proportion of offspring. We believe that this is the first direct evidence that extended periods of sexual activity in catarrhine primates may have evolved as a female strategy to confuse paternity.

Keywords: primates; extended receptivity; concealed ovulation; paternity confusion; infanticide; socioendocrinology

1. INTRODUCTION

Anthropoid primates differ from the general mammalian pattern in the loss of a well-defined period of sexual activity or oestrus (Hrdy & Whitten 1987; Martin 1992). This is particularly evident in the catarrhines (Old World monkeys, apes and humans), in which ovarian cycles are generally characterized by long follicular phases and extended periods of mating, with the result that the usual tight synchronization between ovulation and copulation is abolished (Hrdy & Whitten 1987; Martin 1992; Nunn 1999; Van Schaik *et al.* 2000). The costs of this phenomenon are clear: desynchronization increases the risk of fertilization occurring with aged gametes, resulting in an increased likelihood of pregnancy failure or embryonic abnormalities (German 1968; Austin 1970). Its possible adaptive significance, however, is less evident. One of the most frequently proposed hypotheses is that it represents part of an evolved female strategy to confuse paternity as a means of reducing the risk of infanticide. Infanticide by males is common among primates, and represents an important source of female reproductive loss (for a review, see Van Schaik 2000). An extended period of sexual activity involving polyandrous mating enables females to dilute paternity among males and render its assessment more difficult (Van Schaik *et al.* 1999, 2000). Since male mammals can probably not recognize offspring directly (Elwood & Kennedy 1994) but have to use other indicators, such as timing of mating relative to

peak female attractivity and proceptivity (e.g. Borries *et al.* 1999*b*; Soltis *et al.* 2000), female polyandry and an extended period of receptivity may affect the males' decisions to commit infanticide (Hrdy 1979; Robbins 1995; Borries *et al.* 1999*b*; Van Schaik *et al.* 1999; Soltis *et al.* 2000).

If females cannot freely select their mates, polyandrous mating will be more difficult to achieve, especially if there is a period of maximum attractivity near ovulation. Under such circumstances, it is hypothesized that effective paternity dilution requires a long mating period and a weakened link between behavioural or morphological landmarks and timing of ovulation, because otherwise the dominant male will monopolize the female during her fertile period (Van Schaik *et al.* 2000). There is circumstantial evidence in favour of this hypothesis. Long follicular phases with long mating periods are found predominantly in those species subject to infanticide by males and in which harassment of females by males is observed, i.e. catarrhines (Van Schaik *et al.* 2000). There is also some indirect evidence that the timing of ovulation is highly variable in these species (Nunn 1999; Van Schaik *et al.* 2000), and that exposure to additional males leads to longer mating periods (e.g. Cords 1984; Takahata *et al.* 1994).

To date, however, there is no direct evidence that the female's reproductive physiology and behaviour lead to paternity confusion, even where males attempt to monopolize sexual access to females for days on end. One of the principal reasons for this stems from the lack of suitable methodology for monitoring sexual behaviour in relation to the time of ovulation, and subsequent paternity analysis, in primates living under natural conditions. Hence, opportunities to assess the extent to which females

are able to influence mating outcome have hitherto been virtually non-existent.

Here, we describe studies carried out in a group of free-ranging Hanuman langurs using behavioural assessment combined with recently developed non-invasive endocrine and genetic analyses of faecal material to provide the first direct evidence for a relationship between loss of defined oestrus and paternity confusion in primates. Specifically, the hypotheses that we set out to test were as follows: first, that the timing of ovulation within the receptive period is variable and can occur at any stage of the receptive phase; second, that males are unable to predict or detect the time of ovulation, i.e. that ovulation is effectively concealed; and third, that non-dominant males sire a substantial proportion of offspring.

The Hanuman langur (*Semnopithecus entellus*) provides us with a good opportunity to investigate the phenomenon of paternity confusion and its underlying proximate mechanisms. The species shows a high flexibility in social organization, forming multi-female groups that can contain both single and multiple males (Sommer *et al.* 1992; Borries 1997). In multi-male groups females usually mate with all males during an extended period of receptivity (Borries *et al.* 1999*a,b*, 2001). Moreover, there is also extensive documentation of infanticide by male Hanuman langurs (Sommer 1994; Borries 1997), as well as recent genetic evidence that this behaviour is adaptive, forming part of a strategy to increase male reproductive success (Borries 1997; Borries *et al.* 1999*b*). Under these circumstances, a female counter-strategy to safeguard her own reproductive investment, probably through paternity confusion, would be predicted.

2. MATERIAL AND METHODS

(a) *Animals and study site*

The study was conducted on a group of wild Hanuman langurs inhabiting a semi-evergreen forest in the foothills of the Siwalik mountains at Ramnagar, southern Nepal ($27°44'$N, $84°27'$E, altitude 300m). The habitat is characterized by a marked seasonal variation in climate, with a clear rainy season from mid-June to the beginning of October, which is associated with an increase in food abundance (Koenig *et al.* 1997). As a consequence, the langur population at Ramnagar demonstrates a seasonal pattern of reproduction, with conceptions being confined to the period from July to November, and the majority of births taking place between February and May (Koenig *et al.* 1997; Ziegler *et al.* 2000).

Individual members of the study group have been monitored, and demographic data of the group have been documented from 1992 to 1997 (Nikolei & Borries 1997). At the beginning of this study, the group comprised 26 animals, including four adult males and 15 adult females. Based on reproductive history derived from the long-term demographic records, 10 females expected to exhibit ovarian cycles and to conceive during the study period were selected as focal animals (Ziegler *et al.* 2000). The group composition of adult animals remained stable during the study period, except for one male that left the group two months after the onset of the study and a short-term (19 day) absence of one of the remaining males.

(b) *Behavioural observations*

The behavioural and endocrine data presented in this study were collected during the 1996 mating season (June to November). Study females were followed daily from dawn to dusk, and data on female proceptivity, receptivity and mating activities were collected using *ad libitum* sampling during continuous recordings (Martin & Bateson 1993) and focal-animal sampling (30 min h^{-1}) during a total of *ca.* 3000 h of observation. Focal females were observed without interruption throughout the whole daylight period (on average 12 h) during their receptive phases. Receptive periods were defined as periods during which females were engaged in proceptive and/or receptive behaviours, i.e. sexual solicitations directed to males, copulation attempts and/or copulations (Sommer *et al.* 1992). A receptive period was classified as such if the sexual behaviours mentioned above were shown for a minimum of 3 consecutive days and, if lasting longer, were without interruptions of more than 2 days. Observations of displacement interactions were used to establish the dominance relationships between the three group males, according to the procedure described by Borries *et al.* (1991).

(c) *Collection of faecal samples and progestogen analysis*

During individual receptive periods ($n=15$), faecal samples were collected from the females on an almost daily basis (see Ziegler *et al.* 2000). Fresh faecal samples were homogenized, and a portion (3–5 g) placed in tubes containing 15 ml of greater than 90% ethanol (Ziegler *et al.* 2000), in which they were stored at 4–8 °C until shipment to the laboratory.

Faecal samples were twice extracted in watery ethanol and methanol as described by Ziegler *et al.* (2000), and subsequently measured for immunoreactive pregnanediol-3-glucuronide (iPdG) by microtitreplate enzyme immunoassay according to procedures previously described and validated for monitoring ovarian function in Hanuman langurs (Heistermann *et al.* 1995; Ziegler *et al.* 2000). The patterns of faecal progestogens were then used to determine the lengths of individual cycles and their component phases, as well as to assess the timing of ovulation. In this respect, a sustained rise in faecal iPdG levels above a defined threshold value (two standard deviations above the mean of the preceding three to five baseline values) was used to indicate the onset of the post-ovulatory (luteal) phase of each ovarian cycle (figure 1) (Ziegler *et al.* 2000). Correspondingly, levels below this threshold indicated the interluteal or follicular phase of the cycle. The timing of ovulation was assessed as the day of the defined faecal progestogen increase corrected for a time lag of 3 days (see inserts of figure 1), as inferred from a separate study on captive langurs (Heistermann *et al.* 1995). Data on cycle length and its component phases, as well as dates of ovulation, may include an error of 1 day.

(d) *Genetic analysis*

For determination of paternity, faecal samples were collected during the 1997 birth season from mother–infant pairs and adult males in the study group and in adjacent groups. Fresh samples were stored in greater than 90% ethanol at 4–8 °C until later analysis. Faeces was extracted and, for paternity exclusion, five informative microsatellite loci (D16S420, D12S67, SCA1, D17S79 and D4S2366) originally established for humans were subsequently amplified by polymerase chain reaction according to the procedures described by Launhardt *et al.* (1998). A male was treated as a non-father whenever he could be excluded by at
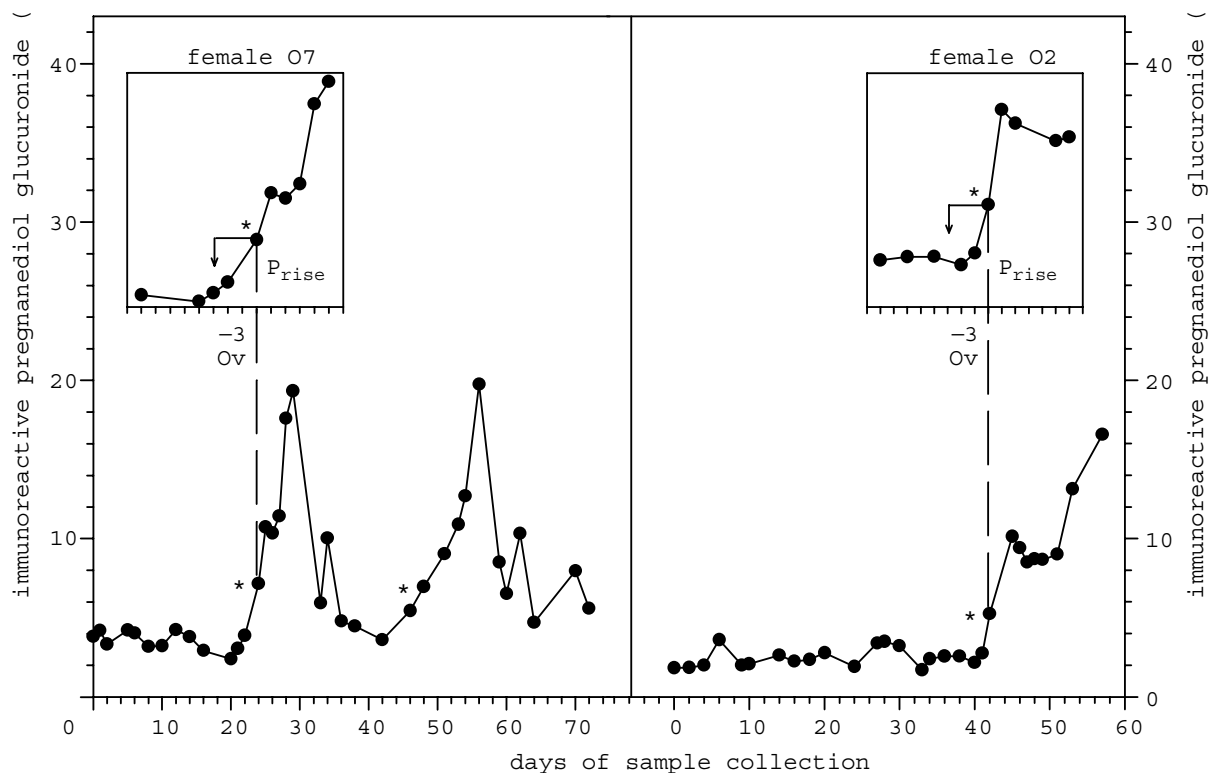
Figure 1. Faecal progestogen profiles throughout individual ovarian cycles in two female Hanuman langurs (O7 and O2). The data demonstrate that pre-ovulatory and post-ovulatory phases of the cycle can be clearly differentiated by changes in faecal progestogen concentrations. The timing of ovulation (Ov) is deduced by identifying the day on which faecal iPdG levels increase above a defined threshold value (P_{rise}, indicated by asterisks; see § 2c) and correcting for an appropriate time lag of 3 days (inserts; see § 2c).

least one microsatellite system. If a male could not be excluded by one or more microsatellite systems, he was considered to be the likely father. The average paternity-exclusion probability for all five loci combined was 88.8% (Launhardt *et al*. 1998).

(e) *Statistical analysis*

Examination of the relationship between male and female sexual behaviour, and their distribution throughout the receptive period were made using Spearman's rank-correlation test and one-way repeated measures analysis of variance (ANOVA), respectively. The distribution of ovulations within receptive periods was examined using the chi-squared test. Kruskal–Wallis one-way ANOVA was used to compare female solicitations towards individual males.

3. RESULTS

(a) *Ovarian-cycle characteristics and duration of receptive periods*

Out of the 10 females studied, nine showed regular periods of receptivity and mating. According to the faecal progestogen profiles (for example, figure 1), eight of these females also exhibited ovulatory cycles and conceived (Ziegler *et al*. 2000). In all, 15 cycles were recorded, and in six of these complete data on overall cycle length and follicular and luteal phase lengths could be compiled (table 1).

Each ovulatory cycle was associated with periods of female behavioural receptivity and the occurrence of

Table 1. Data on durations of ovarian cycles, component cycle phases and receptive periods in wild Hanuman langurs.

(All values are given in days; $n = 6$ for data on cycle length and component phases, $n = 15$ for data on receptive periods.)

	mean (median)	standard deviation	range
cycle length	27.0 (26.5)	4.6	21–34
follicular phase	12.8 (13.0)	3.6	8–18
luteal phase	14.2 (13.0)	2.8	12–19
receptive period	9.2 (10)	3.4	4–15

mating activities. As shown in figure 2a, individual receptive periods were highly variable in length, ranging from 4 days to 15 days with an average value of mean ± s.e.m. = 9.2 ± 3.4 days (median 10 days). Two-thirds (66.1%) of all combined days of receptivity shown during the mating season overlapped with each other, with up to six females displaying receptivity simultaneously (figure 3). Three-quarters of the individual receptive phases were associated with a period of consortship during which the female was monopolized by a male. As illustrated in figure 3, however, these periods of monopolization were relatively short (mean ± s.e.m. duration = 2.2 ± 1.3 days, range of 0.5–6 days, $n = 19$) in
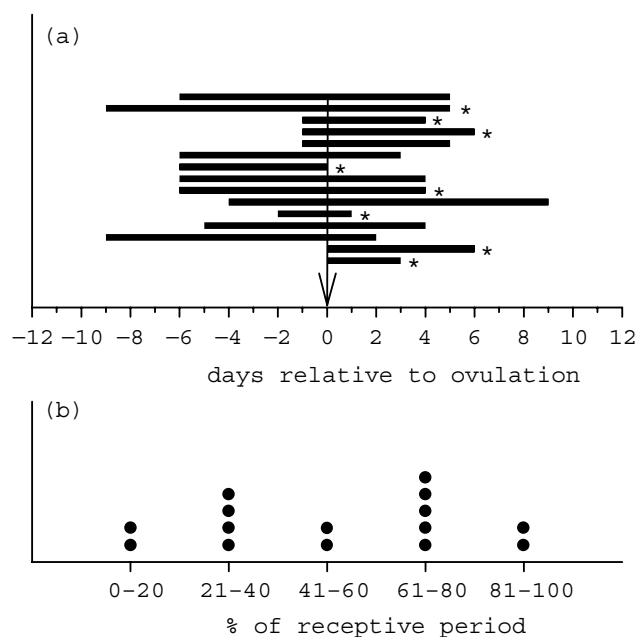
Figure 2. (*a*) Duration of individual receptive periods (horizontal black bars) (mean duration 9.2 days, range 4–15 days) and timing and (*b*) distribution (number) of ovulations in relation to the receptive phases in female Hanuman langurs. The vertical arrow in (*a*) indicates the time at which ovulation occurs; asterisks indicate receptive periods in which conception occurred.
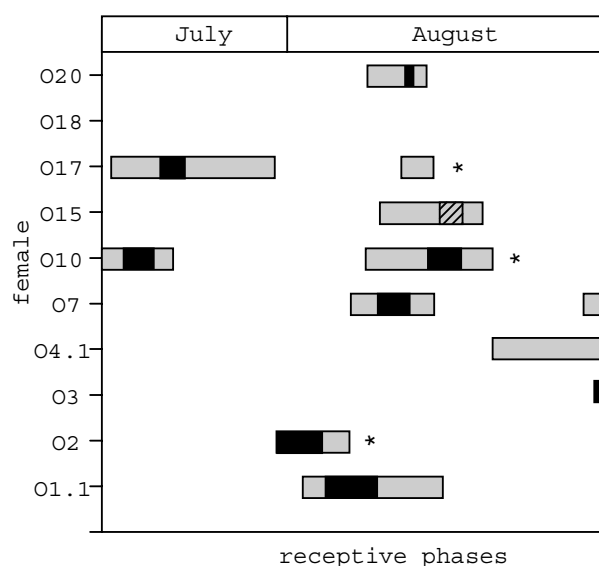

Figure 3. Temporal distribution of receptive phases and periods of female monopolization by study males, from mid-July to the end of August in the 1996 mating season. Boxes represent individual receptive phases. Black and hatched inserts indicate periods of monopolization by the dominant and the third-ranking males, respectively. Asterisks indicate receptive periods in which conception occurred. This figure illustrates the variable timings of monopolizations during individual receptive phases by the dominant male, the length of these monopolizations and, in particular, that the dominant male was switching between simultaneously receptive females.

comparison with the overall period of receptivity; switching of the male between receptive females was often observed.

(b) *Timing of ovulation and distribution of sexual behaviour in relation to the time of ovulation*

Paternity confusion requires that the timing of ovulation within the receptive period varies and that males are unable to predict it. We tested these hypotheses using the faecal iPdG profiles to indicate the time of ovulation (figure 1). We found that in each ovulatory cycle ovulation was restricted to the receptive phase. As predicted, however, the time at which ovulation occurred within this period was extremely variable, ranging from the first day to the last day of the receptive phase (figure 2*a*). As a consequence, the probability of ovulation did not vary significantly with the stage of the receptive period ($\chi^2 = 2.67$, d.f. $= 4$, $p = 0.62$; figure 2*b*).

In order to investigate the extent to which ovulation was concealed from the males, the relationship between female proceptive behaviour and male copulatory responses throughout the receptive period and their distributions in relation to the time of ovulation were examined. The data indicate a positive correlation between the number of copulations and the number of female solicitations for each receptive period ($r_s = 0.73$, $p < 0.03$, $n = 15$). However, as shown in figure 4*a*, the relative frequency of female solicitations did not vary significantly during the period of receptivity ($F = 0.715$, d.f. $= 13$, $p = 0.73$), nor was there evidence for a peak in female proceptive behaviour at the time of ovulation. Furthermore, we found that the frequency of copulation, expressed both in relative numbers (figure 4*b*) and in

terms of per female solicitation (figure 4*c*), was highest at the beginning of the receptive phase and declined progressively thereafter ($r_s = -0.60$, $p < 0.03$ and $r_s = -0.85$, $p < 0.001$, respectively), irrespective of the time of ovulation. The frequency of copulatory activity was thus relatively low around the time of ovulation, and, in accordance with the pattern of female proceptive behaviour, there was no peak in copulation frequency at this time.

(c) *Female solicitations and paternity outcome in relation to male rank*

In order to examine whether female langurs actively solicited copulations from a specific male, we investigated the distribution of female proceptive behaviour towards the three group males (91.2% of observed solicitations were towards these males, while the remaining 8.8% were directed at males from adjacent groups). With 53.2% ($n = 630$), compared with 26.1% ($n = 309$) and 11.9% ($n = 141$) for the two subordinate males, the dominant male received the most solicitations ($H = 23.27$, d.f. $= 2$, $p < 0.01$). However, the relative proportion of female solicitations during the fertile phase (2 days before ovulation until the day of ovulation) compared with the non-fertile phase of the receptive period was similar for all males (dominant male: $39.5 \pm 7.4\%$; subordinate males: $30.9 \pm 7.1\%$ and $29.3 \pm 9.7\%$; $H = 3.08$, d.f. $= 2$, $p = 0.216$).

In order to determine individual male reproductive success, we assessed paternity outcome based on the faecal DNA data. In our study group, eight conceptions
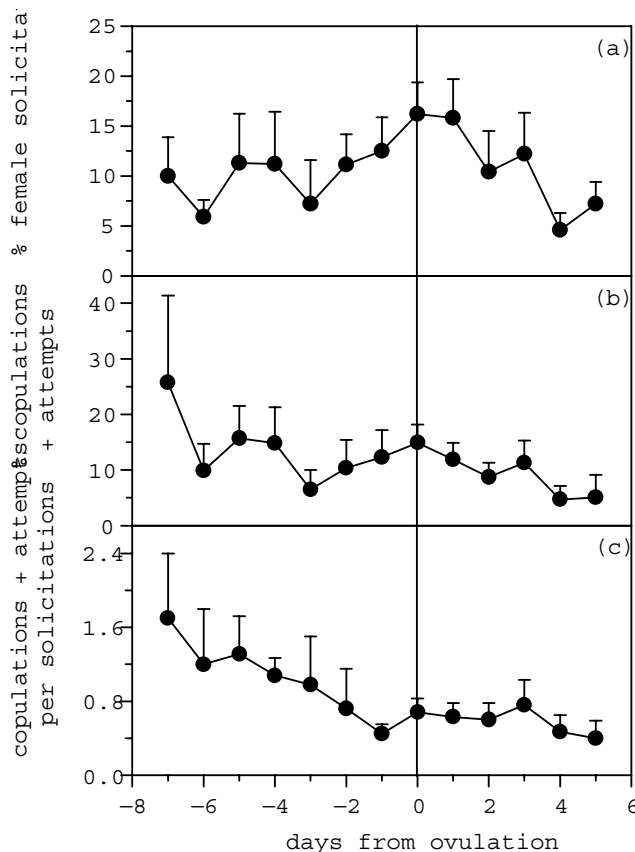
Figure 4. Distributions of (*a*) female proceptive behaviour (solicitation) and male copulatory behaviour expressed as either (*b*) relative frequencies or (*c*) per female solicitation in relation to the time of ovulation. Figures for copulations and attempts represent interactions of all adult males (*n* = 3–4) with each female during the course of her receptive period. Data are plotted as mean ± s.e.m. for the total number of receptive periods available (*n* = 15 around ovulation, decreasing outwards according to the lengths of individual receptive periods).

Table 2. Paternity in relation to male rank and degree of female monopolization.

(Female monopolization is defined as days on which the male maintained close proximity to the receptive female. The individual percentages given represent the proportions of the total number of monopolization days performed by all group males.)

male	rank	days of female monopolization (%)	number of offspring
MX	1	84.6	1
M74	3→2[a]	12.8	0
M24	2→3[a]	2.6	3[b]
outgroup male	—	0.0	1

[a] Males M74 and M24 exchanged ranks in August 1996 (middle of the mating season).
[b] One offspring was fathered during tenure in the rank 2 position.

occurred, with seven resulting in the birth of live offspring (Ziegler *et al*. 2000). For two out of these seven infants paternity could not be assessed because no faecal samples were available. Out of the five infants in which paternity was determined, only one was fathered by the dominant male, despite the finding that he exhibited the highest degree of female monopolization (table 2). Three infants were sired by one of the subordinate males, and one was fathered by a male from an adjacent group (table 2).

4. DISCUSSION

In this study of free-ranging Hanuman langurs we provide, to our knowledge, the first direct evidence that extended receptivity in catarrhine primates is related to a mechanism of paternity confusion. Specifically, we have been able to show that female langurs living in a multi-male group have long and variable receptive periods in which the timing of ovulation is not only highly variable but also concealed from the males, and also that non-dominant males sire a substantial proportion of offspring. In doing so, we have demonstrated that females are able

to influence mating outcome, and we have also provided information on the proximate mechanism underlying paternity confusion in primates.

Faecal hormone analysis has previously been used to assess female reproductive status in field studies on various primate species (for a review, see Whitten *et al*. 1998), including the Hanuman langur (Ziegler *et al*. 2000). Here, we demonstrate that the method is useful not only for characterizing ovarian cycles but also for providing more precise information on the timing of ovulation. An overall cycle length of 26–27 days comprising a follicular phase of 13 days and a luteal phase of 13–14 days in our study females agrees with figures derived from hormonal studies on captive animals (Lohiya *et al*. 1988; Heistermann *et al*. 1995) and is in line with field data on inter-oestrus intervals previously reported for this (Borries *et al*. 2001) and other (Sommer *et al*. 1992) populations of the species.

Each of the 15 ovulatory cycles studied was accompanied by a period of female proceptive and receptive behaviour during which females solicited copulations from all group males. As predicted, and in line with the paternity-confusion hypothesis, these periods were markedly variable in length (range 4–15 days) and, with an average duration of 9–10 days (cf. Borries *et al*. 2001), were also significantly longer than in females living in one-male groups at Jodphur (4 days; Sommer *et al*. 1992) in which paternity confusion is less of an option. Furthermore, females in our study group showed a substantial overlap in receptive phases, with as many as six females being receptive at the same time. While this is probably a direct consequence of the combination of an extended receptive period and a seasonally restricted period of ovarian cyclicity (Ziegler *et al*. 2000), rather than a female strategy to synchronize 'oestrus' (cf. McClintock 1983), it nevertheless facilitates paternity manipulation by enabling females to escape from continuous monopolization by the dominant male (Van Schaik *et al*. 1999). Our data on monopolization patterns showed that the dominant male monopolized females for only a limited period of, on average, 2–3 days, after which he usually switched

to a new female. Such a short period of monopolization would be to the male's advantage if he could ensure that it coincided with the fertile phase of the female's cycle (e.g. baboons; Hausfater 1975) since this would maximize his chances of successful fertilization but reduce the costs associated with long consortships and high frequencies of mating (cf. Alberts *et al.* 1996; Domb & Pagel 2001). Our data on copulation patterns, however, show that this is not the case for Hanuman langurs at Ramnagar. Here, the males are unable to detect the time at which ovulation occurs, and are therefore unable to align their periods of monopolization with the fertile phase of the female's cycle. Thus, extended and overlapping periods of receptivity in which ovulation is effectively concealed provide a situation in which paternity confusion will occur.

That paternity in our study group is, in fact, confused can be reasonably assumed from the genetic data showing that paternity is not restricted to the dominant male and that non-dominant (and occasionally extra-group) males sire a substantial proportion of offspring (see also Launhardt *et al.* 2001). Since, however, female langurs do not solicit copulations from a specific male, as seen for example in capuchins (Janson 1984) and lemurs (Pereira & Weiss 1991; Richard 1992), we consider it unlikely that females are attempting to pre-determine paternity outcome. This results in a situation in which paternity will be confused to both sexes, but nevertheless, by achieving this, the female not only ensures that no male is able to discern which offspring he has sired but also effectively biases paternity away from the dominant male, since all males that mate with her have a reasonable probability of fathering her offspring. On an individual basis, however, the dominant male is still more successful, since, for the Ramnagar population as a whole, 57% of all offspring born in multi-male groups are fathered by the highest-ranking male (Launhardt *et al.* 2001). Reproductive success in the dominant male is therefore sufficiently high to outweigh the costs of attaining the dominant position and attempted female monopolization and its defense (see above).

In catarrhine primates living in multi-male groups, such as the Hanuman langurs in this study, paternity confusion has been proposed as serving to reduce the risk of infanticide by males (Hrdy 1979; Van Schaik *et al.* 2000). In the Ramnagar population, infanticide accounts for 31%–63% of infant mortality (Borries 1997), and has been shown to represent an evolved strategy to optimize male reproductive success (Borries 1997; Borries *et al.* 1999*a*). Since a male's decision to commit infanticide appears to be highly dependent on his past mating history with the mother (Borries *et al.* 1999*a*), a female strategy to mate polyandrously with all available males (including those from adjacent groups: this study; Launhardt *et al.* 2001), and thereby maximize the number of possible sires through paternity confusion, should be highly adaptive in preventing male infanticidal behaviour. Moreover, since putative fathers in langurs are highly engaged in infant protection against attacking (potentially infanticidal) males (Borries *et al.* 1999*b*), by confusing paternity females would also ultimately benefit from a reduction in the infanticidal risk posed by males who were not present during the female's mating (conception) period (cf.

Borries *et al.* 1999*b*; Soltis *et al.* 2000). It thus seems reasonable to assume that extended periods of receptivity coupled with polyandrous mating and an effective mechanism of paternity confusion have evolved in langurs living in multi-male groups as a female counter-strategy to reduce the overall risk (and actual frequency) of infanticide (cf. Borries & Koenig 2000).

Alternative explanations are, however, also possible. Paternity confusion or manipulation could represent a form of cryptic female choice (Eberhard 1996; Keil & Sachser 1998), a way of improving control of group composition (Rubenstein 1986) or a means of increasing paternal care (Whitten 1987). Whilst the alternatives are not necessarily mutually exclusive, and may in some cases be important, there is as yet no convincing evidence for them in langurs. In many other catarrhine species there is circumstantial evidence for unpredictable ovulation and its anti-infanticide function (Van Schaik *et al.* 2000), but systematic evaluation of all the alternatives is now needed.

In conclusion, female langurs (and probably other anthropoid primates) have developed the ability to manipulate paternity to safeguard their own reproductive success. This, together with a complex social organization, may explain why sexual behaviour in anthropoid primates, including humans, has been largely uncoupled from ovarian activity, thus departing from the usual mammalian pattern.

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